

## Tamias quadrimaculatus.

By Robin G. Clawson, Joseph A. Clawson, and Troy L. Best

Published 2 June 1994 by The American Society of Mammalogists

### *Tamias quadrimaculatus* Gray, 1867

#### Long-eared Chipmunk

*Tamias quadrimaculatus* Gray, 1867:435. Type locality "California, Michigan Bluff (Gruber) [Placer County—Merriam, 1897: 203]."

*Tamias macrorhabdotes* Merriam, 1886:25. Type locality "Sierra Nevada mountains of central California" (Blue Canyon, Placer County—Miller, 1924:207).

**CONTEXT AND CONTENT.** Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Genus *Tamias*, Subgenus *Neotamias*. The genus *Tamias* contains 25 species (Levenson et al., 1985; Wilson and Reeder, 1993). *T. quadrimaculatus* is monotypic (Hall, 1981).

**DIAGNOSIS.** *Tamias quadrimaculatus* (Fig. 1) is identified as a member of the *townsendii* species group by its large size and white-edged tail, but the long ears, narrow and shallow rostrum, long nasals, and relatively great zygomatic width distinguish it from all other California members of the group (Johnson, 1943). In addition to these characters, its dark color, long and slender ears, and conspicuous, white postauricular patches distinguish *T. quadrimaculatus* from all other chipmunks (Grinnell and Storer, 1924). Except for *T. senex*, *T. quadrimaculatus* is the largest chipmunk in Nevada (Hall, 1946).

The baculum of *T. quadrimaculatus* differs from those of *T. bulleri*, *T. palmeri*, *T. panamintinus*, *T. speciosus*, *T. townsendii*, and *T. umbrinus* by having a longer shaft and a proportionately shorter tip. In addition, there is a wide angle between the tip and shaft (White, 1953). This angle is less obtuse than that found in *T. cinereicollis* (Burt, 1960).

**GENERAL CHARACTERS.** *Tamias quadrimaculatus*, one of the reddest species of *Tamias*, has large ears, a white-edged tail (Allen, 1890), and a large white postauricular patch. In winter pelage (October–May), the top of the head is sayal brown mixed with grayish white and fuscous (general tone is near cinnamon drab), bordered on the sides with fuscous. The sides of the nose are clay color or sayal brown. The dark facial stripes are fuscous black. The malar stripe (below the eye) extends beneath the ear and connects with the large and creamy white postauricular patches. The submalar stripe is shaded with mikado brown, it is broad, and it reaches back beneath the ear to the postauricular patch. The pale facial stripes are grayish white. The ears are fuscous or fuscous black on the anterior one-half and grayish white on the posterior one-half. The median dorsal stripe is fuscous black; other dark stripes are fuscous and mixed with mikado brown. The median pair of pale stripes is grayish white, often mixed with sayal brown; the outer pair is creamy white. The sides are sayal brown to snuff brown. The rump and thighs are neutral gray, mixed with fuscous, and sprinkled with grayish white. The hind feet are deep pinkish-cinnamon or pinkish buff; the forefeet are colored similarly, but paler. Dorsally, the tail is fuscous black overlaid with grayish white (the ochraceous bases of the hairs sometimes show); ventrally, the tail is ochraceous tawny or mikado brown, bordered with fuscous black and edged with pale smoke-gray. The underparts are grayish white (color nomenclature follows Ridgway, 1912—Howell, 1929).

Summer pelage (August) is similar to winter pelage, but the upperparts are more ochraceous (less grayish) in general tone. The anterior region of the back, including the median pair of pale stripes, nearly always is strongly washed with cinnamon. The sides are sayal brown to mikado brown. The rump and thighs are more buffy (less grayish) in summer, with a faint wash of cinnamon buff (color nomenclature follows Ridgway, 1912—Howell, 1929).

Autumn pelage (October) is similar to postbreeding pelage,

except the rufous suffusion of the flanks is darker, and the gray of the rump occupies the posterior one-half of the dorsal region; the anterior one-half is rufous and forms a scapular mantle. The ears are more reddish in front, the dark facial stripes are darker, and the malar stripe terminates in a dusky patch beneath the ear (Allen, 1890). Autumn molt occurs in October; the winter pelage first covers the tail and then proceeds to the rump (Howell, 1929).

Averages and ranges of external measurements (in mm) for males and females, respectively, are: total length, 231 (200–240), 237 (229–245); length of head and body, 138 (125–150), 141 (125–150); length of tail, 94 (85–106), 96 (88–118); length of hind foot (dry), 34.5 (33.8–36.3), 35.1 (33.8–36.3); length of ear from crown (dry), 14.9 (13.7–16.1), 15.3 (12.6–17.5—Johnson, 1943). Length of tail is ca. 64–70% of length of head and body (Allen, 1890; Johnson, 1943), and length of ear (from crown on dry skin) averages >10% of length of head and body (Johnson, 1943). Average mass of adults is 81 g (range, 73–105—Howell, 1929). Mass (in g) of males and females, respectively, from Merced Grove of Big Trees, Mariposa Co., California, are 78.6 (74.1–89.0) and 91.9 (81.0–105.0—Hall, 1946). Males (131.8 mm) are significantly smaller than females (138.7 mm) in length of head and body (Levenson, 1990).

The skull of *T. quadrimaculatus* (Fig. 2) is small (Johnson, 1943). The postorbital processes are directed laterally (Jameson and Peeters, 1988), the zygomatic arches flare widely, the rostrum is narrow and shallow, the nasals are long, the braincase is short and broad, the upper rows of teeth are widely spaced, and individual teeth are small (Hall, 1946; Johnson, 1943). Averages and ranges of cranial measurements (in mm) for males and females, respectively, are: condylobasal length, 33.0 (32.5–33.7), 33.3 (32.5–33.9); greatest length of cranium, 36.8 (36.1–37.5), 37.2 (36.5–38.1); zygomatic breadth, 20.7 (20.3–21.1), 20.7 (20.2–21.4); breadth of cranium, 16.7 (16.3–17.1), 16.6 (16.2–17.1); depth of cranium, 11.5 (11.1–12.1), 11.6 (11.4–11.9); interorbital breadth, 8.9 (8.3–9.6), 8.9 (8.5–9.3); length of nasals, 12.5 (11.9–13.2), 12.5 (11.8–13.0); depth of rostrum, 5.6 (5.5–5.8), 5.6 (5.3–5.9); length of incisive foramina, 2.4 (2.2–2.7), 2.7 (2.4–3.0); length of lower toothrow, 5.7 (5.4–6.1), 5.8 (5.4–6.0—Johnson, 1943).

**DISTRIBUTION.** *Tamias quadrimaculatus* is endemic to the northern Sierra Nevada of California and Nevada (Fig. 3; Johnson, 1943), and it inhabits upper transition and lower Canadian life zones at elevations of 960–2,250 m (Grinnell, 1933; Grinnell and



FIG. 1. A *Tamias quadrimaculatus* at Glacier Point, Yosemite Valley, California. Photograph by W. L. Huber; courtesy of the Museum of Vertebrate Zoology, University of California, Berkeley.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias quadrimaculatus* from Aspen Valley, 1,920 m, Yosemite Park, Tuolumne Co., California (male, Museum of Vertebrate Zoology, University of California, Berkeley 23308). Greatest length of cranium is 36.2 mm. Photographs by T. H. Henry.

Storer, 1924; Howell, 1929). In California, *T. quadrimaculatus* ranges from the vicinity of Lake Almanor, Plumas Co., southward to the vicinity of Bass Lake, Madera Co. (Holdenried, 1940; Johnson, 1943; Sutton, in press). In Nevada, *T. quadrimaculatus* occurs in the vicinity of Lake Tahoe (Hall, 1946).

**FOSSIL RECORD.** *Tamias* evolved by the early Miocene (Black, 1972). No fossils of *T. quadrimaculatus* are known.

**FORM AND FUNCTION.** As in all members of the subgenus *Neotamias*, the dental formula is  $c\ 1/1, i\ 0/0, p\ 2/1, m\ 3/3$ , total 22 (Howell, 1929; Ingles, 1965). Dorsal guard hairs of *T. quadrimaculatus* have a maximum length  $<13$  mm, and a width of  $59\ \mu$ . The distal end of the guard hair widens into a spatulate tip. Pigmentation is prominent in the distal pale region, and the distal dark band is 3 mm in length (Mayer, 1952).

Summer molt apparently takes place late in summer. An adult male on 12 August and an adult female on 10 August had nearly completed molt; the rump was the only part of the body showing

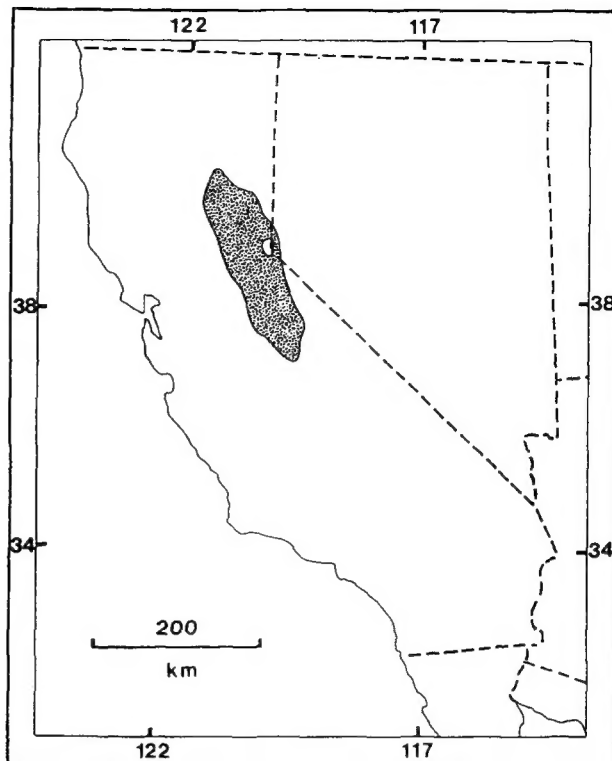


FIG. 3. Distribution of *Tamias quadrimaculatus* in western North America (Hall, 1981).

worn winter pelage. Two breeding females on 8 August and one on 13 August were in worn winter pelage, with scarcely any indication of the beginning of the molt (Howell, 1929).

The hippocampus of the central nervous system may be involved in hibernation (Hooper et al., 1985). In captivity, *T. quadrimaculatus* had a daily range in body temperature from  $32.6^{\circ}\text{C}$  during sleep to  $39.2^{\circ}\text{C}$  during activity. If forced to move around at night, *T. quadrimaculatus* quickly attained a rectal temperature of  $37^{\circ}\text{C}$  and became more responsive, but if left alone its temperature soon dropped to  $\leq 34^{\circ}\text{C}$ . *T. quadrimaculatus* kept at  $3-4^{\circ}\text{C}$  for 2-5 days with food did not become torpid, lose weight, or have rectal temperatures  $<30^{\circ}\text{C}$  (Cade, 1963).

The baubellum (Fig. 4) appears thick in all parts except the sharply tapered base. The base-shaft angle is acute, with the base turned back to a line parallel with the shaft. The shaft bends to the right ca.  $30^{\circ}$  in relation to the base, and the tip is bent ca.  $25^{\circ}$  further to the right. The heel is small and the tip has a large keel. The curved, narrow flanges extend to the distal end of the shaft. The side of the tip opposite the keel is convex. Averages and ranges of measurements (in mm) of the baubellum are: width of base, 0.67 (0.62-0.72); length of shaft, 0.93 (0.91-0.94); depth of shaft, 0.37 (0.36-0.39); length of tip, 0.76 (0.72-0.81); length of keel, 0.34 (0.33-0.36); angle of the tip-shaft,  $136^{\circ}$  ( $135-137^{\circ}$ —Sutton, 1982).

The baculum of *T. quadrimaculatus* (Fig. 4) has a low keel 0.2-0.3 mm in length, the tip is 1.5-1.6 mm in length, and the angle formed by the tip and shaft is  $122-126^{\circ}$ . The length of the shaft is 4.6-4.9 mm, the base is wider than the shaft, and the distal one-third of the shaft is compressed laterally (Sutton, in press; White, 1953). Approximate sizes (in mm) of the reproductive organs of sexually active males are: length of testis, 16; length of seminal vesicle, 10; maximum diameter of bulbourethral gland, 8; maximum diameter of prostate gland, 5; maximum thickness of cauda epididymis, 4 (Tevis, 1955).

**ONTOGENY AND REPRODUCTION.** During late April and early May, male *T. quadrimaculatus* pursue females, and most breeding takes place in the first 2 weeks of May (Storer et al., 1944). In captive long-eared chipmunks, mating activity is 2 weeks in duration. The gestation period is ca. 31 days (Ross, 1930). Nests may be constructed under buildings (Storer et al., 1944) and in hollow trees (Brand, 1970, 1974). One litter of two to six young

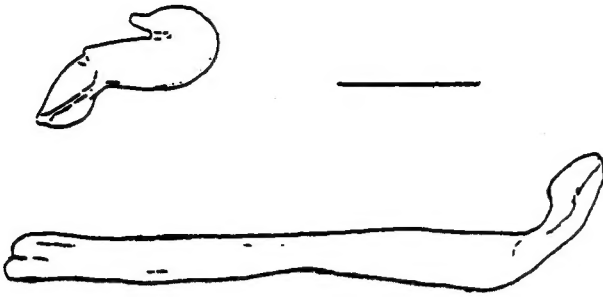


FIG. 4. Genital bones of *Tamias quadrimaculatus*: left-lateral view of baubellum (above); right-lateral view of baculum (below). The line is 1 mm in length (modified from Sutton, in press).

(average, 4.4) is produced each year (Grinnell and Storer, 1924; Tevis, 1955). Young are born from May (Ross, 1930; Stephens, 1906) to July (Stephens, 1906). In the Sierra Nevada of California, the majority of young are born 1–14 June (Storer et al., 1944). Young that are one-third grown resemble adults in coloration (Allen, 1890). Immatures that are two-thirds of adult size may be present in August. By early September, the young are almost fully grown (Storer et al., 1944).

**ECOLOGY.** *Tamias quadrimaculatus* lives in chaparral (Grinnell, 1933; Sutton, in press), brushfields (Tevis, 1955), and open ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and mixed-coniferous forests (Ingles, 1965; Tevis, 1955). Usually, its habitat includes fallen logs, stumps, snags, rocks, litter (Barrett et al., 1980), and brush patches (Grinnell, 1933; Grinnell and Storer, 1924). *T. quadrimaculatus* is found in denser forests than most of its congeners (Stephens, 1906). At the northern end of Lake Tahoe, its habitat is comprised of open places in mature timber, where felled trees of large diameter afford shelter among manzanita bushes (*Arctostaphylos patula*—Hall, 1946). In Deanes Valley, Plumas Co., California, *T. quadrimaculatus* was present on a steep, forested hillside above a stream. Here there were scattered bushes and logs in an open second-growth forest that consisted of *Abies concolor*, *Libocedrus decurrens*, *Pinus lambertiana*, *P. ponderosa*, *Pseudotsuga menziesii*, *Quercus kelloggii*, *Ceanothus cordulatus*, *C. integriramus*, *Ribes*, and *Arctostaphylos patula* (Brand, 1970). In another logged area, tangles of dead limbs provided homes for a large number of long-eared chipmunks. Incense cedar (*L. decurrens*) and white fir (*A. concolor*) were the most numerous trees, with ponderosa and sugar pines (*P. lambertiana*) nearly as abundant. Black oak (*Q. kelloggii*) was the only deciduous tree present in appreciable numbers. Gooseberry (*Ribes roezlii*) covered most of the area not shaded by trees, whereas deerbrush (*C. integriramus*) was more widely distributed (Holdenried, 1940).

*Tamias quadrimaculatus* feeds on a variety of fruits and seeds (Grinnell and Storer, 1924), especially seeds of conifers such as sugar pine (Smith, 1943; Van Dersal, 1938) and Douglas fir. When conifer seeds are not available, long-eared chipmunks may subsist on hypogeous fungi (Jameson and Peeters, 1988). In one study, the yearly dietary volume of fungi was 66% and included *Boletus* and *Clitocybe* (Fogel and Trappe, 1978; Tevis, 1952). Whitethorn (*C. cordulatus*) also may be a major food in some seasons and comprised 88% of the food volume in one study. Other foods included the seeds and flowers of manzanita, leaves, pulp and whole seeds of gooseberries, bits of reddish bark from trunks of ponderosa pine, pupae and eggs of insects, and a garter snake (*Thamnophis ordinoides*) that had been crushed by an automobile (Tevis, 1953b). In Plumas Co., it consumed pupae of California tortoise-shell butterflies (*Nymphalis californica*). It did not select hairy caterpillars, but instead searched in trees and bushes for chrysalids (Tevis, 1953a). Diet varies among seasons. The percentage volume and percentage frequency (in parentheses) of the types of food consumed for spring, summer, and autumn, respectively, are: seeds, 17 (28), 16 (20), 10 (23); fungi, 34 (59), 76 (89), 88 (97); leaves, 22 (44), trace (4), trace (4); flowers, 11 (18), 0 (0), 0 (0); fruits, 0 (0), 5 (7), 0 (0); arthropods, 15 (38), 3 (9), 2 (3); flesh, 1 (14), trace (2), 0 (0—Tevis, 1953b). Diet also varies among habitats. In a burned conifer forest replaced by black oak and deerbrush, *T. quadrimaculatus* consumed 63% seeds (percent volume) and 37% fungi. In a burned



FIG. 5. Karyotype of a female *Tamias quadrimaculatus* from Lake Almanor, Plumas Co., California. Roman numerals indicate the type of chromosome: I, large metacentric; II, submetacentric; III, large acrocentric; IV, small metacentric; V, small acrocentric. The number of chromosomes of each type is noted (modified from Sutton and Nadler, 1969).

conifer forest replaced by mixed brush, it ate 72% fungi, 13% seeds, and 15% miscellaneous items, and in a logged conifer forest, it ate 98% fungi and 2% insects (Tevis, 1952).

Unrecovered caches of conifer seeds often sprout, thus aiding in reforestation. However, when clumps of shrub seedlings appear after a forest fire, long-eared chipmunks may contribute to generation of dense brushfields that hinder the return of timber (Tevis, 1953b). Thus, *T. quadrimaculatus* also may play a role in preventing re-seeding of conifer forests (Smith and Aldous, 1947).

In captivity, *T. quadrimaculatus* eats almonds, walnuts, acorns of *Quercus lobata*, rolled oats, ground barley, and seeds of cantaloupes, pumpkins, gourds, and sunflowers. It also may consume fresh peaches, corn, canned fruits and vegetables (Ross, 1930), rat chow (Hooper et al., 1985), cracked corn, milo maize, barley, pieces of apple, and peanut butter mixed with oatmeal. Apple and a peanut butter-oatmeal mixture is readily eaten, but sunflower seeds are the only food stored in nest boxes. Seeds are shelled before being stored in the bottom of the cotton lining of the nest (Cade, 1963), in forks of branches, or in high nest boxes (Brand, 1970, 1974).

In the Sierra Nevada of California, home ranges of adult males averaged 0.88 ha (range, 0.32–1.84) and those of adult females averaged 0.48 ha (range, 0.32–0.64). Males ranged more widely than females. These data primarily were obtained in the spring during the breeding season; the home range may be different at other times of the year. The home range is large for chipmunks of this body size, perhaps reflecting the active nature of *T. quadrimaculatus*. At all seasons, but especially during breeding time, the ranges of males overlap extensively, with little sign of territoriality. In the breeding season, most males have cuts, especially on the face. Females usually maintain separate home ranges, with slight overlapping of boundaries. If territory is held by individual females, it probably is maintained by constant defensive activities (Storer et al., 1944).

Two-thirds of the females near Bass Lake, Madera Co., California, made maximum movements (the distance between the two most widely separated places of capture) of 120–180 m. Only 14% of females moved >180 m, whereas 48% of males moved at least this far. Only two females moved >240 m, but 15 males moved 270–510 m. The average maximum movement was 137 m for females and 210 m for males. One male made a maximum movement of 216 m, but was captured several other times in traps nearly as widely separated. A male made a maximum movement of 432 m, 6–28 September, yet its first capture on 2 September was only 54 m from its last capture on 5 October. An immature female taken on 10 August was 135 m from its first capture on 9 August. On 15 August, it was taken again at the place of its first capture and on 16 August it was captured 81 m away. The movements of these chipmunks show that they frequently make daily movements of 90–120 m. Observations of foraging chipmunks reveal that they move 30–45 m in 2–3 min (Holdenried, 1940).

In the Sierra Nevada Mountains of California, the active population of *T. quadrimaculatus* rapidly increased in the spring and early summer, as individuals emerged from hibernation. From a density of 0.2/ha in April, long-eared chipmunks attained a peak

of 1.0/ha in June. There was a decrease in July and none were trapped in August, although several were active in the area. This change in density may have been due to the preference at that time for ripening gooseberries over the dry rolled oats, pine nuts, and prunes used to bait traps. However, gooseberries used as bait rarely were successful in attracting chipmunks. The active population decreased in autumn as individuals entered hibernation or left the area. Density dropped from 0.2/ha in September to 0.04/ha in early November. Males probably emerge from hibernation earlier than females. The number of females, as indicated by trap records, increased slowly during the spring. Most of them apparently were active by 15 May, but unmarked individuals were caught until 15 June. All females trapped in June were lactating, indicating that they had been active for at least 1 month. Subadults made up the bulk of the autumn population, as adults apparently entered hibernation before the young (Storer et al., 1944).

*Tamias quadrimaculatus* occupies the same habitats as *Sorex*, *Spermophilus beecheyi*, *Tamiasciurus douglasii*, *Thomomys bottae*, *Chaetodipus californicus*, *Peromyscus boylii*, *P. maniculatus*, *Neotoma cinerea*, and *Microtus montanus* (Holdenried, 1940). On the eastern slope of the Sierra Nevada near Truckee, Nevada Co., California, *T. quadrimaculatus*, *T. amoenus*, *T. senex*, and *T. speciosus* are sympatric, i.e., populations in breeding condition exist within the home range of individuals of congeners (Sharples, 1983). On the lower slopes north of the Yosemite, *T. quadrimaculatus* occurs below the range of *T. senex* and seems to replace *T. merriami* (Merriam, 1897). *T. quadrimaculatus*, although occupying a lower zone than *T. senex* where the two occur together, is nevertheless a more boreal species, restricted to the upper one-half of the transition zone, whereas *T. sonomae* is not found above the lower one-half of the transition zone (Johnson, 1943).

Reconstruction of the ranges of *Tamias* at the height of the last glaciation reveals that *T. palmeri*, *T. quadrimaculatus*, and *T. umbrinus* were then in contact. *T. quadrimaculatus* may have been in contact with the *T. umbrinus*-*T. palmeri* lineage during interglacial and glacial periods, and thus cannot be derived from that lineage by refugial isolation. *T. quadrimaculatus*, however, although presently sympatric with *T. senex*, was isolated from that species in a montane coniferous forest refugium during the most recent glacial period, and thus could have been derived from the *T. townsendii* lineage during periods of glacial isolation. *T. quadrimaculatus* is parapatric with *T. umbrinus* in the Sierra Nevada today. Niche partitioning among these species probably is a result of the nature of different glacial and interglacial habitats to which the various species became adapted. Habitats of *T. quadrimaculatus* and *T. umbrinus*, located in the same geographic area, were more similar to each other than to habitats of the *townsendii* species group farther west and north along the coast. Adaptation to different habitats thus permitted *T. senex* and *T. quadrimaculatus* to respond to different aspects of the environment they now share, and to effectively partition its resources (Hoffmann, 1981).

A dead rattlesnake (*Crotalus*) had the tail of an entire long-eared chipmunk sticking out of its mouth (Grinnell and Storer, 1924). Other reptiles and several species of birds and mammals may use *T. quadrimaculatus* as a source of food, but this has not been reported.

Plague (*Yersinia pestis*) has been detected in *T. quadrimaculatus*, but this chipmunk shows heterogeneity for resistance and susceptibility (Nelson, 1980). Near Quincy, Plumas Co., California, 56% of *T. quadrimaculatus* had an average of 2.4 fleas/chipmunk. Fleas recovered included *Catallagia sculleni*, *Diamanus montanus*, *Monopsyllus eumolpi*, *M. ciliatus*, and *Oropsylla idahoensis* (Tevis, 1955). Additional ectoparasites are the ticks *Dermacentor andersoni* and *Haemaphysalis leporispalustris* (Furman and Loomis, 1984).

*Tamias quadrimaculatus* has been marked for identification by amputation of toes (Holdenried, 1940). Identification collars also have been used; these were made of colored porcelain beads strung on copper wire and fastened around the neck of chipmunks (Cade, 1963).

**BEHAVIOR.** *Tamias quadrimaculatus* remains close to the ground; it is active on the forest floor and along logs and rock outcroppings (Grinnell and Storer, 1924; Johnson, 1943). This chipmunk has quick movements and displays sudden-prolonged immobility after each change of position; its pelage coloration blends into the mixed background. When frightened, it seeks safety in dense

brush or in hollow logs rather than in trees (Grinnell and Storer, 1924). It is terrestrial, but will climb trees (e.g., Grinnell, 1933; Grinnell and Storer, 1924; Stephens, 1906). One was seen ca. 15 m above the ground on a dead stub (Grinnell and Storer, 1924). In Deanes Valley, California, a litter of five half-grown young occupied a hollow, partially dead, oak snag. The entrance was near the top, ca. 6 m above the ground. Young were observed going into the hollow tree for the night, descending during the day. Another litter of five young was in a hollow oak snag ca. 90 m from the previous nest. The young spent the night in the nest and left it during the day. The mother also was seen entering the nest at dusk (Brand, 1970).

The call note of the *T. quadrimaculatus*, which is a "whsst" or "psst," is sharper than the call of *T. speciosus* (Grinnell and Storer, 1924; Miller, 1944). *T. quadrimaculatus* spends a greater percentage of time chipping or chucking in trees, than in bushes, on logs, rocks, or the ground. Calls include the chip, chipping, chuck, and chatter (in courtship). When *T. quadrimaculatus* chips, it sometimes flips its tail upward (Brand, 1970). Vocalization rates in Plumas Co. are: chips/min, 19 (range, 5–55); chips/burst, 1.8 (1.0–4.2); bursts/min, 11 (5–24); length of syllable (in s), 0.070 (0.040–0.095); interval between chips within bursts (in s), 0.155 (0.050–0.305). Frequency ranges (in kilocycles) are: bottom of upsweep, 1.5 (1.0–4.0); top of upsweep, 12.5 (10.0–15.5); bottom of downsweep, 8.0 (4.0–11.5—Brand, 1976). The sonograms of chips of *T. quadrimaculatus* show that the lower part of the upsweep, beginning at 1.5–2.0 kilocycles, is faint and occasionally absent. After a short break in the sound, the main part of the upsweep begins at 3–4 kilocycles and rises at a steady, slow rate. The average length of the upsweep is 0.05-s longer than other *Tamias*. In 87% of the syllables, there also was a downsweep. The downsweep dropped more slowly than in other species, but it did not go low. Chips always are given in bursts, commonly in bursts of one to three, and the interval between chips within a burst often is short (Brand, 1970).

In its natural habitat, *T. quadrimaculatus* is active from late March to mid-November (Storer et al., 1944) and hibernates during winter (Jameson, 1964; Jameson and Mead, 1964). However, in captivity and under moderate winter conditions, it does not enter deep hibernation. In captivity, one *T. quadrimaculatus* consistently hoarded seeds and slept in isolation from other chipmunks. Although its body temperature remained >30°C, the long-tailed chipmunk became progressively less active as the winter advanced and tended to become lethargic during the prolonged periods of inactivity. These changes in activity became obvious on 20 November, when it did not emerge from the nest box until 0945 h, 2 h after other captive species of chipmunks had become active. On 25 November, it did not appear until 1300 h and remained outside for only 1 h. The *T. quadrimaculatus* was not seen outside the nest box on 2 December, although that night it had a rectal temperature of 34°C. From this date until 9 January, it often remained inside the nest box all day, emerging if at all, for 30–45 min at ca. 1400–1500 h. During these exits, *T. quadrimaculatus* seemed more interested in drinking than in collecting seeds. During this period, it kept a large store of 200–300 g of shelled sunflower seeds in the bottom of the nest. After 9 January, it began to appear regularly for short periods each afternoon, but never for >1–2 h at a time. Although the *T. quadrimaculatus* frequently was observed at night during this time, it was never torpid and the lowest rectal temperature was 32.6°C (Cade, 1963). In the warmer months of the year, *T. quadrimaculatus* is active by sunrise (Grinnell and Storer, 1924).

On one occasion, an immature male and female *T. quadrimaculatus* were observed making squeaking sounds under a white fir tree. Both were covered with ants and fleas (Storer et al., 1944). Other long-tailed chipmunks have been observed vigorously scratching; one pulled a piece of hard outer wood from a decayed log and repeatedly dragged its body through the rooted wood inside. Because the ground adjacent was still wet from snowmelt, the chipmunk probably used the dust from the rotted wood to remove insect pests (Grinnell and Storer, 1924).

Reactions of *T. quadrimaculatus* to noxious models and edible mimics were examined in the laboratory. The food items consisted of a yellowish mixture of white flour, egg yolk, and milk, rolled into balls with a diameter of 0.3 cm, and allowed to dry. The mimics were unaltered, but the models had a few grains of quinine hydrobromide placed in their center. When given a choice, the chipmunks ate 2.68 times more the dough-ball mixture than laboratory rat chow. They exhibited aversive reactions after sampling quinine-laced



dough balls. Chipmunks encountering a simulated Batesian mimicry complex with the models and mimics randomly distributed foraged extensively only when mimics represented 99% of the population. If the models and the mimics were nonrandomly distributed, however, extensive foraging occurred when mimics were 70% of the complex. Groups of chipmunks that did not forage extensively were tested to see how rapidly they could detect a favorable change in the frequency of mimics. Success in escaping detection for the mimics was closely linked to how well sampling behavior was eliminated in the prior treatment. Animals that experienced nonrandom distributions seemed more adept in detecting a favorable change (Nonacs, 1985).

**GENETICS.** *Tamias quadrimaculatus* has the type B karyotype of *Tamias* (Fig. 5). The diploid karyotype contains 38 chromosomes including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969). In a study involving 20 allozymes, *T. quadrimaculatus* had an average heterozygosity of 0.0758 and four polymorphic loci (glucose-6-phosphate dehydrogenase, 6-phosphogluconate dehydrogenase, and two loci for red cell phosphoglucose mutase—Levenson et al., 1985).

**REMARKS.** *Tamias quadrimaculatus* belongs to the *townsendii* group, but is not closely related to any species in that group. Its closest affinity may be with *T. sonomae*, as shown by similarities of the skull and color of the back in summer pelage (Howell, 1929). Using morphologic and pelage characters, *T. quadrimaculatus* was placed in the *townsendii* group with *T. dorsalis*, *T. merriami*, *T. obscurus*, *T. ochrogenys*, *T. senex*, *T. siskiyou*, *T. sonomae*, and *T. townsendii* (Howell, 1929). Characteristics of bacula placed *T. quadrimaculatus* with the *quadrivittatus* group, which includes *T. quadrivittatus*, *T. ruficaudus*, and *T. cinereicollis* (White, 1953). Phenetic analyses of morphologic data have placed *T. quadrimaculatus* in the same cluster as *T. bulleri*, *T. canipes*, *T. durangae*, *T. merriami*, *T. obscurus*, *T. ochrogenys*, *T. senex*, *T. siskiyou*, *T. sonomae*, and *T. townsendii*. Cladistic analyses of electrophoretic data have placed *T. quadrimaculatus* in the same cluster as *T. amoenus*, *T. cinereicollis*, *T. merriami*, *T. palmeri*, *T. senex*, *T. siskiyou*, *T. sonomae*, *T. townsendii*, and *T. umbrinus* (Levenson et al., 1985; Nadler et al., 1985).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Levenson et al., 1985; Nadler et al., 1969, 1977; Wilson and Reeder, 1993). However, there are indications that *Eutamias* and *Tamias* may be distinct genera, e.g., divergence in the late Miocene (Ellis and Maxson, 1979; Hafner, 1984), differences in pattern of dorsal stripes, structure of the hyoid, chromosomes, dental formulas, bacula (Hoffmeister, 1986), microcomplement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

*Tamias* is from the Greek *tamias* meaning a storer or distributor. The specific epithet is from the Latin *quadrus* meaning fourfold and *maculatus* meaning spotted (Jaeger, 1955). *T. quadrimaculatus* also has been referred to as the Sacramento chipmunk (Allen, 1890) and the four-banded chipmunk (Elliot, 1905).

We thank L. L. Thornton, A. M. Coffman, and other personnel in the Interlibrary Loan Department at Auburn University R. B. Draughon Library for assistance in obtaining articles from other institutions, and K. A. Howard for preparing Fig. 3. J. B. Armstrong, J. R. Callahan, F. S. Dobson, R. B. Forbes, and W. L. Gannon critically evaluated an early draft of the manuscript. This is journal article no. 15-923342 of the Alabama Agricultural Experiment Station.

#### LITERATURE CITED

- ALLEN, J. A. 1890. A review of some of the North American ground squirrels of the genus *Tamias*. Bulletin of the American Museum of Natural History, 3:45-116.
- BARRETT, R. H., ET AL. 1980. California wildlife and their habitats: western Sierra Nevada. United States Department of Agriculture, Forest Service, General Technical Report, PSW-37:1-439.
- BLACK, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). Evolutionary Biology, 6:305-322.
- BRAND, L. R. 1970. Vocalizations and behavior of the chipmunks (genus *Eutamias*) in California. Ph.D. dissert., Cornell University, Ithaca, New York, 128 pp.
- . 1974. Tree nests of California chipmunks (*Eutamias*). The American Midland Naturalist, 91:489-491.
- . 1976. The vocal repertoire of chipmunks (genus *Eutamias*) in California. Animal Behaviour, 24:319-335.
- BURT, W. H. 1960. Bacula of North American mammals. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 113:1-76.
- CADE, T. J. 1963. Observations on torpidity in captive chipmunks of the genus *Eutamias*. Ecology, 44:255-261.
- ELLIOT, D. G. 1905. A check list of mammals of the North American continent the West Indies and the neighboring seas. Field Columbian Museum Publication 105, Zoological Series, 6:1-701.
- ELLIS, L. S., AND L. R. MAXSON. 1979. Evolution of the chipmunk genera *Eutamias* and *Tamias*. Journal of Mammalogy, 60:331-334.
- FOGEL, R., AND J. M. TRAPPE. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science, 52:1-31.
- FURMAN, D. P., AND E. C. LOOMIS. 1984. The ticks of California (Acari: Ixodida). Bulletin of the California Insect Survey, 25:1-239.
- Gray, J. E. 1867. Synopsis of the species of burrowing squirrels (*Tamias*) in the British Museum. Annals and Magazine of Natural History, series 3, 20:434-436.
- GRINNELL, J. 1933. Review of the Recent mammal fauna of California. University of California Publications in Zoology, 40:71-234.
- GRINNELL, J., AND T. I. STORER. 1924. Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. University of California Press, Berkeley, 752 pp.
- HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3-23, in The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.
- HALL, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, 710 pp.
- . 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1-600 + 90.
- HOFFMANN, R. S. 1981. Different voles for different holes: environmental restrictions of refugial survival of mammals. Pp. 25-45, in Evolution today (G. G. E. Scudder and J. L. Reveal, eds.). Proceedings of the Second International Congress of Systematic and Evolutionary Biology, Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 486 pp.
- HOFFMEISTER, D. F. 1986. Mammals of Arizona. The University of Arizona Press and The Arizona Game and Fish Department [Tucson], 602 pp.
- HOLDENRIED, R. 1940. A population study of the long-eared chipmunk (*Eutamias quadrimaculatus*) in the central Sierra Nevada. Journal of Mammalogy, 21:405-411.
- HOOPER, D. C., S. M. MARTIN, AND J. M. HOROWITZ. 1985. Temperature effects on evoked potentials of hippocampal slices from euthermic chipmunks, hamsters and rats. Journal of Thermal Biology, 10:35-40.
- HOWELL, A. H. 1929. Revision of the American chipmunks (genera *Tamias* and *Eutamias*). North American Fauna, 52:1-157.
- INGLES, L. G. 1965. Mammals of the Pacific states: California, Oregon, and Washington. Stanford University Press, Stanford, California, 506 pp.
- JAEGER, E. C. 1955. A source-book of biological names and terms. Third ed. Charles C Thomas Publisher, Springfield, Illinois, 323 pp.
- JAMESON, E. W., JR. 1964. Patterns of hibernation of captive *Citellus lateralis* and *Eutamias speciosus*. Journal of Mammalogy, 45:455-460.
- JAMESON, E. W., JR., AND R. A. MEAD. 1964. Seasonal changes in body fat, water and basic weight in *Citellus lateralis*, *Eutamias speciosus* and *E. amoenus*. Journal of Mammalogy, 45:359-365.
- JAMESON, E. W., JR., AND H. J. PEETERS. 1988. California mammals. University of California Press, Berkeley, 403 pp.

- JOHNSON, D. H. 1943. Systematic review of the chipmunks (genus *Eutamias*) of California. University of California Publications in Zoology, 48:63-147.
- LEVENSON, H. 1990. Sexual size dimorphism in chipmunks. Journal of Mammalogy, 71:161-170.
- LEVENSON, H., R. S. HOFFMANN, C. F. NADLER, L. DEUTSCH, AND S. D. FREEMAN. 1985. Systematics of the Holarctic chipmunks (*Tamias*). Journal of Mammalogy, 66:219-242.
- MAYER, W. V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. The American Midland Naturalist, 48:480-512.
- MERRIAM, C. H. 1886. Description of a new species of chipmunk from California (*Tamias macrorhabdotes* sp. nov.). Proceedings of the Biological Society of Washington, 3:25-28.
- . 1897. Notes on the chipmunks of the genus *Eutamias* occurring west of the east base of the Cascade-Sierra system, with descriptions of new forms. Proceedings of the Biological Society of Washington, 11:189-212.
- MILLER, A. H. 1944. Specific differences in the call notes of chipmunks. Journal of Mammalogy, 25:87-89.
- MILLER, G. S., JR. 1924. List of North American Recent mammals 1923. Bulletin of the United States National Museum, 128: 1-673.
- NADLER, C. F., R. S. HOFFMANN, AND D. M. LAY. 1969. Chromosomes of the Asian chipmunk *Eutamias sibiricus* Laxmann (Rodentia: Sciuridae). Experientia, 25:868-869.
- NADLER, C. F., R. S. HOFFMANN, AND H. LEVENSON. 1985. Biochemical and morphological relationships among Holarctic chipmunks. Acta Zoologica Fennica, 170:19-23.
- NADLER, C. F., R. S. HOFFMANN, J. H. HONACKI, AND D. POZIN. 1977. Chromosomal evolution in chipmunks, with special emphasis on A and B karyotypes of the subgenus *Neotamias*. The American Midland Naturalist, 98:343-353.
- NELSON, B. C. 1980. Plague studies in California—the roles of various species of sylvatic rodents in plague ecology in California. Proceedings of the Vertebrate Pest Conference, 9:89-96.
- NONACS, P. 1985. Foraging in a dynamic mimicry complex. The American Naturalist, 126:165-180.
- RIDGWAY, R. 1912. Color standards and color nomenclature. R. Ridgway, Washington, D.C., 340 pp.
- ROSS, R. C. 1930. California Sciuridae in captivity. Journal of Mammalogy, 11:76-78.
- SHARPLES, F. E. 1983. Habitat use by sympatric species of *Eutamias*. Journal of Mammalogy, 64:572-579.
- SMITH, C. F. 1943. Relationship of forest wild life to pine reproduction. The Journal of Wildlife Management, 7:124-125.
- SMITH, C. F., AND S. E. ALDOUS. 1947. The influence of mammals and birds in retarding artificial and natural reseeding of coniferous forests in the United States. Journal of Forestry, 45: 361-369.
- STEPHENS, F. 1906. California mammals. The West Coast Publishing Company, San Diego, 351 pp.
- STORER, T. I., F. C. EVANS, AND F. G. PALMER. 1944. Some rodent populations in the Sierra Nevada of California. Ecological Monographs, 14:165-192.
- SUTTON, D. A. 1982. The female genital bone of chipmunks, genus *Eutamias*. The Southwestern Naturalist, 27:392-402.
- . In press. Problems of taxonomy and distribution in four species of chipmunks in northern California. The Southwestern Naturalist.
- SUTTON, D. A., AND C. F. NADLER. 1969. Chromosomes of the North American chipmunk genus *Eutamias*. Journal of Mammalogy, 50:524-535.
- TEVIS, L., JR. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. Journal of Mammalogy, 33:198-205.
- . 1953a. An outbreak of *Nymphalis californica* near Lake Almanor, California. The Pan-Pacific Entomologist, 29:201-202.
- . 1953b. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy, 34:316-324.
- . 1955. Observations on chipmunks and mantled squirrels in northeastern California. The American Midland Naturalist, 53:71-78.
- VAN DERSAL, W. R. 1938. Native woody plants of the United States: their erosion-control and wildlife values. United States Department of Agriculture, Miscellaneous Publication, 303:1-362.
- WHITE, J. A. 1953. The baculum in the chipmunks of western North America. University of Kansas Publications, Museum of Natural History, 5:611-631.
- WILSON, D. E., AND D. M. REEDER (EDS.). 1993. Mammal species of the world: a taxonomic and geographic reference. Second of the world: a taxonomic and geographic reference. Second ed. Smithsonian Institution Press, Washington, D.C., 1206 pp.

Editors of this account were J. ALDEN LACKEY and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.

R. G. CLAWSON, J. A. CLAWSON, AND T. L. BEST, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESSE HALL, AUBURN UNIVERSITY, ALABAMA 36849-5414.